Generic Relationships Within the Tribes Cratocentrini and Phasgonophorini (Hymenoptera: Chalcididae)

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Abstract.—According to most recent classification, the subfamily Chalcidinae is divided into four tribes: Brachymeriini, Chalcidini, Cratocentrini, and Phasgonophorini. It has been suggested that the tribes Phasgonophorini and Cratocentrini are sister groups and together they form the sister group to a monophyletic group consisting of Brachymeriini and Chalcidini. A cladistic study was conducted to test the relationship between Cratocentrini and Phasgonophorini and to establish the generic relationships, using all known taxa in each tribe. *Brachymeria, Chalcis,* and *Dirhinus* were used as outgroups. Parsimony analysis using the branch and bound search option of PAUP (Ver. 3.1.1), resulted in 14 minimum length trees. None of the trees could be rooted to make Cratocentrini and Phasgonophorini sister groups. Reanalysis of data after successive weighting of characters resulted in a single most parsimonious tree that is identical to one of the original 14 trees. This tree was selected as the preferred hypothesis. These results corroborate the relationships for tribes in Chalcidinae suggested from my previous analysis of chalcidid phylogeny. In addition this study established the generic relationships within Cratocentrini and Phasgonophorini for the first time. The results suggest that *Megachalcis* and *Trigonurella* are the basal lineages of tribes the Cratocentrini and Phasgonophorini, respectively. Because these two genera were not used to represent the tribes in my previous cladistic analysis, the effect of taxon sampling on my chalcidid phylogeny was tested by including these two taxa in the analysis. This analysis showed no effect of taxon sampling on previous phylogenetic analysis. Since this analysis used a separate set of characters than the family level phylogeny analysis, the two data sets were combined and resulting data matrix of 41 taxa and 65 characters was analyzed. This analysis resulted in 14 minimum length trees and successive weighting gave 10 minimum length trees one step longer than any of the 14 minimum length trees from equally weighted data. There is some disagreement between the phylogenetic hypothesis resulting from this analysis for Chalcididae and results of my previous analysis of family phylogeny. This illustrates the effect of biased taxon and character sampling on the results of phylogenetic analysis.

Cratocentrini and Phasgonophorini (Hymenoptera: Chalcididae) are two morphologically distinct groups within the subfamily Chalcidinae. Host records (available only for few species) indicate that the species of both tribes are parasites of wood boring beetle larvae, an unusual host asssociation in Chalcididae (Boucek 1988). They are among the largest chalcidids, varying from 4 to 20 mm. in length. Cratocentrini are distinctive among chalcidids in having an elongated ovipositor which is extended beyond the short syntergum (Fig. 56). Although the majority of Phasgonophorini also have a long ovipositor, the syntergum has extended concealing the elongated ovipositor sheaths (Figs. 55, 57). Both groups were extensively studied by Steffan (1950a, 1950b, 1956, 1959, and 1973). At present each tribe consists of eight genera, all distributed in the tropical areas of the world.

Steffan (1959) suggested that Cratocentrini and Phasgonophorini evolved from

the same "stem". He hypothesized that their specialized abdomens were convergently evolved as a result of ovipositing into similar types of hosts. Boucek (1988) stated that these two tribes were sister groups and formed a sister clade to Chalcidini + Brachymeriini but he did not provide any character evidence.

My previous study of higher level phylogeny of Chalcididae (Wijesekara 1997) indicated that Cratocentrini and Phasgonophorini are not closely related. Phasgonophorini is the sister group to Brachimeriini, and these two tribes plus Haltichellinae, Dirhininae, and Epitraninae form the sister group to Cratocentrini (Fig. 74). However my study of family phylogeny used only two examplars of Cratocentrini and Phasgonophorini. Both tribes consist of eight genera, and it therefore seemed that a study of generic relationships among all known genera of Cratocentrini and Phasgonophorini would be useful not only to establish generic relationships within the tribes but also to test the opposing hypotheses regarding the relationship between these two tribes.

TAXONOMIC HISTORY

Many taxa included in Cratocentrini and Phasgonophorini were described in the nineteenth century and classified within different taxonomic groups. Masi (1944) placed them all within the subfamily Brachymeriinae. Both tribes were established by Steffan (1950a, 1950b).

Phasgonophorini

Steffan (1950b) established the Phasgonophorini to include *Phasgonophora* Westwood 1832, *Trigonura* Sichel 1865, *Stypiura* Kirby 1883, *Megalocolus* Kirby 1883, and *Stenochalcis* Masi 1929. He also described a new genus, *Parastypiura* within Brachymeriinae. He suggested that the tribe consisted of two groups of genera: the *Phasgonophora* group, with abdominal tergite I larger than the tergite II (*Phasgonophora* and *Trigonura*), and the *Stypiura* group,

with abdominal tergite I reduced and shorter than tergite II (*Megalocolus, Parastypiura, Stypiura,* and *Stenochalcis*). Steffan (1956) implied that his tribes were natural groups and gave many synonyms for species of *Phasgonophora* and *Cratocentrus.* Steffan (1973) also revised the genera *Stypiura* (six species) and *Parastypiura* (three species) of the Neotropical region. Since Steffan's work, two more genera have been added to the tribe: *Kopinata* and *Trigonurella* (Boucek 1988). At present Phasgonophorini consists of eight genera and 57 species.

Cratocentrini

The genera *Larradomorpha* Stadelmann 1792, *Marres* Walker 1841, and *Acanthochalcis* Cameron 1884 were originally placed in Leucospidae, and *Cratocentrus* Cameron 1907 was originally placed in Haltichellinae. Masi (1944) subsequently referred these genera to Brachymeriinae. Later, Cratocentrini was established to include these genera plus *Macrochalcis* Masi 1945 (=*Allocentrus* Cameron 1911); and *Megachalcis* Cameron 1903 (Steffan 1950b). The tribe was revised by Steffan (1959), who added four new genera, *Spatocentrus, Philocentrus, Acrocentrus,* and *Vespomorpha.* Narendran (1984) synonymized *Allocentrus* with *Megachalcis*, and Boucek (1992) synonymized *Larradomorpha* with *Marres.* At present the tribe consists of eight genera and 23 species.

MATERIAL AND METHODS

Specimens.—This study was carried out using the collection at the United States National Museum of Natural History, Washington D. C. Additional specimens were borrowed from the following institutions: The Natural History Museum, London; University of Calicut, Kerala, India; South African Museum, Cape Town, South Africa; Plant Protection Research Institute, Pretoria, South Africa; and Museum National de Histoire Naturelle, Paris, France.

Taxa Used and Character Selection.—All valid genera of Cratocentrini and Phasgonophorini were included in this study (Appendix 1). In addition, representatives of other major clades of Chalcididae identified in my earlier family level study (Wijesekara 1997) were also included. These taxa served as outgroups for assessing relationships within the tribes Cratocentrini and Phasgonophorini. A representative of Brachymeriini was included because Cratocentrini + Phasgonophorini have been included in Brachymeriinae and Brachymeriini grouped with Phasgonophorini in my previous analysis. Since my previous analysis of family phylogeny indicated that Brachymeriini plus Phasgonophorini form the sister group to a clade consisting of Haltichellinae, Dirhininae and Epitraninae, I also included *Dirhinus* as an outgroup to represent this sister clade. The tree was rooted by including a representative of Chalcidini (*Chalcis*), which the previous analysis suggested to be the most basal lineage in the family.

Comparative morphology was studied for as many species as possible for each genus (See list of Cratocentrini and Phasgonophorini species studied, Appendix 1). Characters that varied among the genera were selected for the analysis. Characters that proved to be synapomorphies for the relevant tribes in my previous study were also included. The generic autapomorphies were not included in the analysis.

Character Analysis.—Cladistic analysis was performed using "Phylogenetic Analysis Using Parsimony" (PAUP), version 3.1.1 (Swofford 1993). The branch and bound search option, which guarantees finding all shortest possible trees, was used. All the multistate characters were treated as unordered (non-additive; Fitch 1971). Although there are many criteria that can be used to order characters I prefer not to assume the ordering of the states in multistate characters prior to cladistic analysis (Wijesekara 1997). ACCTRAN optimization, which favors secondary loss

(reversals) of characters over parallel evolution of characters (convergence), was used to optimize the character states. Sixteen ingroup taxa and three outgroup taxa were coded for 40 characters. The character optimization was studied using MacClade version 3.0 (Maddison and Maddison 1992).

Stability Analysis.—There are different measures of tree stability for phylogenetic hypotheses. These include the branch lengths (Bremer 1994), Bremer support (decay index), and bootstrap values. Bootstrapping (Felsenstein 1985) and Bremer support (Farris *et al.* 1994) provide a better measure of tree stability than the branch length (Bremer 1994).

The degree of character support for various nodes of the phylogenetic tree was evaluated using bootstrap analysis (Felsenstein 1985) and rescaled branch support (decay) index (Bremer 1988, 1994). AutoDecay version 3.0 (Eriksson 1995) was used to calculate the decay indices.

Abbreviations Used in Figures 1–65.— DAS: dorsal axillary surface, FRD: foraminal depression, FRN: frenum, HC: hind coxa, HF: hind femur, HS: horizontally directed spur, HT: hind tibia, HTS: hind tibial spur, LBR: labrum, LS: lateral sulcus, LM: lamella, MAN: mandible, MEP: mesosternal process, MES: mesepisternum, MNS: mesonotal spiracle, MS: malar sulcus, MV: marginal vein, OCE: ocellus, OS: outer spur, PET: petiole, PMV: postmarginal vein, PRE: prepectus, PRM: posterior pronotal margin, PRN: pronotum, PRO: propodeum, SCA: supraclypeal area, SCR: scrobe, SMV: submarginal vein, STV: stigmal vein, TD: tarsal depression, TEG: tegula, TOR: torulus, TR: trocanter, TV: tergite V, TVII: tergite VII, VER: vertex.

RESULTS AND DISCUSSION

Characters Selected

Forty morphological characters were scored for a total of 19 taxa (Table 1). Eight

Table 1. Data matrix for Phasgonophorini and Cratocentrini.

Taxon	Characters			
	1234567890	1234567890	1234567890	1234567890
Chalcis	0011011000	0000000000	0001000100	2000010000
Brachymeria	0021013000	0001002000	0010102001	0010010000
Dirhinus	0001110000	0101101000	1010110100	0000010000
Acanthochalcis	1221112001	1101010001	2101020112	1110002030
Megachalcis	1221112000	1121010101	2100020112	1110012030
Cratocentrus	1221112020	1102010011	2111020112	1110002020
Marres	1221112000	1102010110	2101010112	1110002030
Vespomorpha	1221112000	1102010010	2101010112	1110002040
Spatocentrus	1221112001	1102010110	2111010112	1110012010
Philocentrus	1221112001	1102010010	2111020112	1110002020
Acrocentrus	1221112020	1102010011	2111010112	1110012010
Phasgonophora	2000000011	1111102010	3200100000	0111011000
Trigonura	2000000001	1111102010	3200100000	0111011000
Trigonurella	2100013000	1101102000	3210100000	0010000000
Stypiura	2010001110	1102010010	3200101000	0020111101
Megalocolus	2000001110	1101102010	3200101000	0010211101
Stenochalcis	2100011110	1101102000	3200101000	0020213100
Kopinata	2100001100	1101102010	3200101000	0010111001
Parastypiura	2000001111	1101102010	3200101000	0011011001

of the characters were also used in the previous analysis of family phylogeny. Those characters are indicated by an asterisk (*) following the character number. The characters are described below and measures of fit for each character are given in table 2.

Characteristics of the Head:

1. Size of the labrum.
    0. Large, as broad as base of mandible (Fig. 1).
    1. Half as long as base of mandible (Fig. 2).
    2. Less than half as broad as base of mandible (Fig. 3).

Both tribes have the typical chalcidid condition of an exposed and contiguous labrum. Phasgonophorini has a small labrum whereas Cratocentrini has a relatively larger labrum, intermediate in size between Brachymeriini and Phasgonophorini. Although the structure of the labrum has been used previously for phylogenetic inference within Chalcidoidea (Darling 1988), the size of the labrum has not.

2. Supraclypeal area.
    0. Without a modified bridge with same sculpture as rest of the face (Fig. 3).
    1. Modified to form a bridge, i.e., with different sculpture than rest of the face (Fig. 4).
    2. Toruli located at the anterior margin of the clypeus and the supralypeal area is reduced (Fig. 2).

In Phasgonophorini the antennal toruli are located away from the clypeal margin. The area between the clypeal margin and antennal toruli is sometimes modified forming a bridge of different sculpture between the scrobal base and clypeus. In most species there is a slight indication of this bridge-like structure, but the area is more or less continuous with the rest of the face having same sculpture. In some other groups this is distinctly differentiated. Cratocentrini differs in having the toruli located at the clypeal margin and hence having very reduced supraclypeal area.

3. Malar region.
   0. Without a sulcus or carina (Fig. 3).
   1. A sulcus present (Fig. 5).
   2. A carina present (Fig. 6).

In most chalcidids the malar region has a distinct sulcus running from the ventral margin of the eye to base of the mandible. The sulcus is absent from most Phasgonophorini, present as a sulcus in *Stypiura* and *Chalcis*, and indicated as a carina in Brachymeriini. In Cratocentrini it is traceable and carina-like as in Brachymeriini.

4. Face.
   0. Distinctly convex (Fig. 7).
   1. Concave or flat (Fig. 8).

Most chalcidids have an almost concave face because of the very large scrobal depression extending from eye margin to eye margin. In most Chalcidinae the scrobes are smaller and the face is flat or slightly convex. In Phasgonophorini the face is distinctly convex because it bulges forward from the vertex and eye margin.

5*. Location of the antennal toruli.
   0. Above the level of lower eye margin (Fig. 4).
   1. Below the level of lower eye margin (Fig. 9).

Cratocentrini consistently have the antennal toruli located just below the level of the lower eye margin. Most Phasgonophorini have the toruli located above the eye margin while a few species have the toruli located just below the lower eye margin.

6. Antenna.
   0. Slender and long with funicle segments longer than broad (Fig. 60).
   1. Stout and short with only first funicle segment longer than broad (Fig. 61).

Slender and long antenna are characteristic of most Phasgonophorini. The funicular segments are elongated and of the same width although slightly decreasing in length towards the apex. By contrast, species with stout antenna have the first

funicle segment slender and long and the other segments distinctly shorter and progressively widening towards the apex. Stout and short antenna are characteristic of most Cratocentrini, Brachymeriini and Dirhininae.

7. Antennal scrobe.
   0. More than 2× as long as broad near toruli and parallel sided (Fig. 7).
   1. Less than 2× as long as broad near toruli and almost pear-shaped with a blunt lateral margin (Fig. 4).
   2. More than 2× as long as broad near toruli and pear-shaped with sharp, flange-like lateral margin (Fig. 9).
   3. More than 2× as long as broad near toruli and pear-shaped with a sharp, smooth lateral margin (Fig. 8).

Antennal scrobes are generally well defined in Chalcididae. In Cratocentrini, Phasgonophorini, and Brachymeriini they are deeper than in other chalcidids. This is probably due to forward growth of the frons. The scrobes are longer in Cratocentrini because the toruli are located closer to the clypeal margin below the level of the lower eye margin.

In some Phasgonophorini the antennal toruli are located above the lower eye margin and the scrobal cavity is shorter. In those species the frons, lateral to the margin of the scrobal cavity, is inflected slightly into the cavity giving it a triangular or pear-shaped appearance (Fig. 4). In Phasgonophorini the scrobe cavity is not margined sharply but in *Brachymeria* and Cratocentrini it is sharply margined. The condition in *Brachymeria* is distinctly different from that of Cratocentrini. The sharp margin of *Brachymeria* is smooth and shiny and resembles the condition in Phasgonophorini. The scrobal margin of Cratocentrini is more flange-like and the toruli are located relatively further apart than in Brachymeriini or Phasgonophorini (Fig. 9).
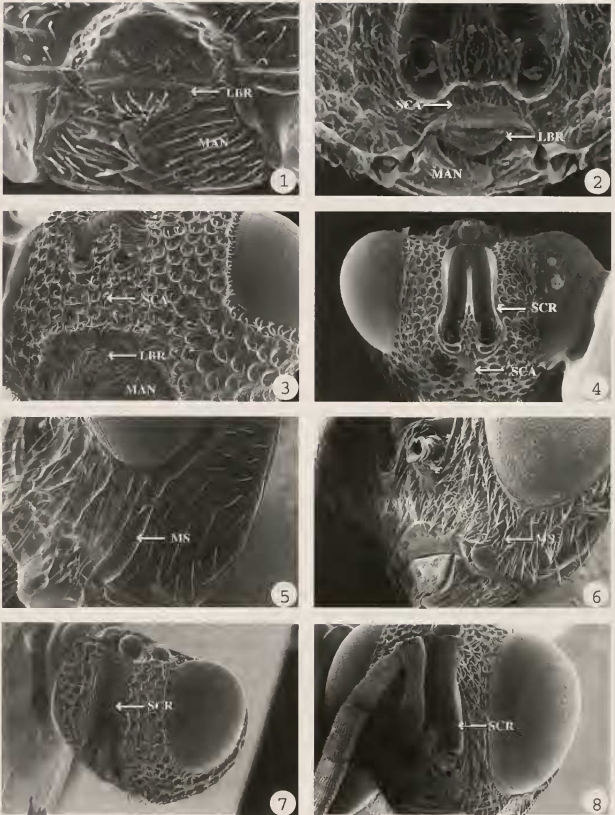
Figs. 1–8. 1–3. Lower front view of face. 1. *Chalcis* sp. 2. *Cratocentrus* sp. 3. *Phasgonophora sulcata*. 4. *Stypiura* sp., front view of face. 5–6. Malar sulcus. 5. *Chalcis* sp. 6. *Brachymeria* sp. 7–8. Face. 7. *Phasgonophora sulcata*. 8. *Brachymeria* sp.

Table 2. Character diagnostics.

Character	Minimum steps	Tree steps	Maximum steps	CI	HI	RI	RC
1	2	2	11	1.000	0.000	1.000	1.000
2	2	4	11	0.500	0.500	0.778	0.389
3	2	4	10	0.500	0.500	0.750	0.375
4	1	1	8	1.000	0.000	1.000	1.000
5	1	2	9	0.500	0.500	0.875	0.438
6	1	2	6	0.500	0.500	0.800	0.400
7	3	5	11	0.600	0.400	0.750	0.450
8	1	1	5	1.000	0.000	1.000	1.000
9	2	4	7	0.500	0.500	0.600	0.300
10	1	5	6	0.200	0.800	0.200	0.040
11	1	2	3	0.500	0.500	0.500	0.250
12	1	2	2	0.500	0.500	0.000	0.000
13	2	2	3	1.000	0.000	1.000	1.000
14	2	4	9	0.500	0.500	0.714	0.357
15	1	1	9	1.000	0.000	1.000	1.000
16	1	1	8	1.000	0.000	1.000	1.000
17	2	2	10	1.000	0.000	1.000	1.000
18	1	3	3	0.333	0.667	0.000	0.000
19	1	3	7	0.333	0.667	0.667	0.222
20	1	3	4	0.333	0.667	0.333	0.111
21	3	3	11	1.000	0.000	1.000	1.000
22	2	2	11	1.000	0.000	1.000	1.000
23	1	4	7	0.250	0.750	0.500	0.125
24	1	2	8	0.500	0.500	0.857	0.429
25	1	1	9	1.000	0.000	1.000	1.000
26	2	3	9	0.667	0.333	0.857	0.571
27	2	2	6	1.000	0.000	1.000	1.000
28	1	1	9	1.000	0.000	1.000	1.000
29	1	1	8	1.000	0.000	1.000	1.000
30	2	2	9	1.000	0.000	1.000	1.000
31	2	2	9	1.000	0.000	1.000	1.000
32	1	2	9	0.500	0.500	0.875	0.438
33	2	3	4	0.667	0.333	0.500	0.333
34	1	2	3	0.500	0.500	0.500	0.250
35	2	3	4	0.667	0.333	0.500	0.333
36	1	2	4	0.500	0.500	0.667	0.333
37	3	3	11	1.000	0.000	1.000	1.000
38	1	1	3	1.000	0.000	1.000	1.000
39	4	4	6	1.000	0.000	1.000	1.000
40	1	2	4	0.500	0.500	0.667	0.333

8. Ocellar triangle.
   0. Not raised above vertex (Fig. 10).
   1. Raised above vertex (Fig. 11).
Most chalcidids have two lateral ocelli located further apart from each other than from the front ocellus and the ocellar triangle is not raised above the level of the vertex. In some Phasgonophorini the ocelli are located close together so that they are equidistant from each other and the ocellar triangle is raised above the vertex.

9. Vertex within ocellar triangle.
   0. Normal, not modified (Fig. 10).
   1. Raised medially between the lateral ocelli (Fig. 11).
   2. Raised lateral to the lateral ocelli (Fig. 12).
In general all three ocelli lie in a triangle on the vertex, with the lateral ocelli lying closer to the posterior margin of the vertex. In some Phasgonophorini the area within the triangle is distinctly raised above the surrounding area resulting in the posterior margin of the vertex rising between the lateral ocelli (Fig. 13). In Cratocentrini the area within the ocellar triangle is sharply raised closer to the lateral ocelli giving the appearance of two sharp spines (Fig. 12).

10. Carina behind lateral ocelli.
   0. Absent.
   1. Present (Fig. 13).
In some Cratocentrini and Phasgonophorini the vertex is separated from the occiput by a short transverse carina just behind the lateral ocelli in the mid dorsal area of the head.

11. Foraminal cavity/depression.
   0. Continuous around occipital foramen (Fig. 14).
   1. Dorsally interrupted (Fig. 13).
Delvare (1992) used this character for within tribe relationships of Chalcidini and considered that the continuous foraminal depression, not delimited by carina or sharp edge, is the ancestral condition for the tribe. The species of Chalcidini that show no evidence of a depression are considered derived. All the genera of the two tribes studied show a distinct foraminal depression.

Characteristics of the mesosoma:

12. Width of the pronotum.
   0. Pronotal width at least 2.5× the median length (Fig. 10).
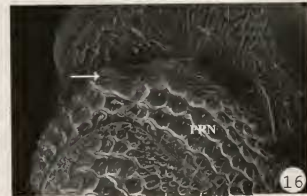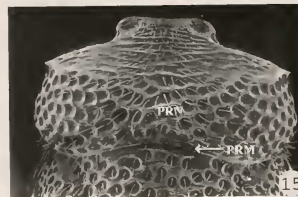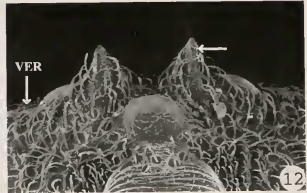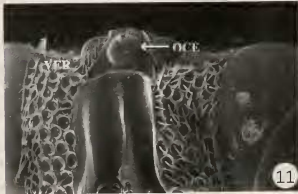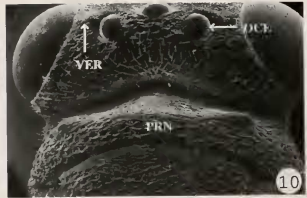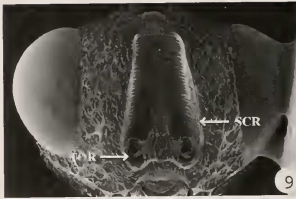
Figs. 9–16. 9. *Cratocentrus* sp., front view of face. 10. *Brachymeria* sp., dorsal view of head and pronotum. 11–12. Ocellar triangle. 11. *Stypiura* sp. 12. *Cratocentrus* sp. 13–14. Head, posterior view. 13. *Phasgonophora sulcata*. 14. *Brachymeria* sp. 15–16. Pronotum (arrows indicate the raised area). 15. *Cratocentrus* sp. 16. *Megachalcis* sp.

1. Pronotal width less than $2.5\times$ the median length (Fig. 15).

Both Phasgonophorini and Cratocentrini have a relatively broad pronotum. In Brachymeriini and Chalcidini the pronotum is distinctly short anterio-posteriorly.

13. Pronotal surface.
 0. Flat (Fig. 15).
 1. Raised lateral to the median line (Fig. 16).
 2. Raised as bump near each posterior lateral margin (Fig. 17).

The plesiomorphic state of the dorsal pronotal surface of Chalcididae is flat without any raised areas. Some groups of Phasgonophorini have the pronotum raised on both sides of the median line resulting in a shallow median furrow on the pronotum (Fig. 16). A bump-like raised area at each lateral corner of the pronotum is another modification shown by some genera of Cratocentrini (Fig. 17). These bumps are very distinct in *Megachalcis*. They are located away from the median line closer to the posterior margin of the pronotum, between the lateral margin and median line.

14. Posterior margin of the pronotum.
 0. Broadly concave (Fig. 10).
 1. Medially triangular (Fig. 18).
 2. Medially rounded (Fig. 15).

The shape of the posterior margin of the pronotum of chalcids varies from broadly concave to emarginate. The most commonly observed condition is a broadly concave posterior margin. This character is probably correlated to the degree to which the head can be directed backwards. In most Phasgonophorini the curvature is so acute that it appears medially triangular and in most Cratocentrini the posterior margin is more rounded (Fig. 15).

15*. Externally visible region of the prepectus
 0. Relatively large and elongated, plate-like (Fig. 19).

1. Reduced to a very thin or knob-like sclerite (Fig. 20).

The chalcidid prepectus is a semi-annular, transverse sclerite. Delvare (1992) found the median process of the prepectus to be phylogenetically informative to resolve Chalcidini relationships. However within Cratocentrini and Phasgonophorini the median process does not vary. Instead the lateral arm of the prepectus near the tegula and the pronotal/mesonotal juncture has twisted to form a small plate-like sclerite that supports the mesothoracic spiracle and separates the mesopleural margin from the mesonotal margin. The size of this exposed plate-like area of the prepectus varies within Chalcididae. In Cratocentrini and Chalcidini the plate-like area is reduced to an extent that it is difficult to observe externally. The reduced state is autapomorphic for Cratocentrini and Chalcidini within Chalcididae. In Phasgonophorini, Brachymeriini, and Haltichellini the plate is distinct externally.

16*. Mesothoracic spiracle.
 0. Covered by postero-lateral margin of pronotum (Fig. 19).
 1. Exposed (Fig. 20).

In most Hymenoptera the pronotal lobe covers the mesothoracic spiracle completely (Gibson 1985). Chalcididae except Cratocentrini have the mesothoracic spiracle covered by the posterior lateral margin of the pronotum.

17*. Relative size and shape of the tegula.
 0. Linear, scond axillary sclerite covered (Fig. 20).
 1. Both ventrally and posteriorly expanded, oval shape, second axillary sclerite of the wing completely covered.
 2. Ventrally expanded, second axillary sclerite of the wing exposed (Fig. 19).

In Chalcidini and Cratocentrini the tegula is not modified, it is pear shaped and extends from the anterio-lateral margin of pronotum to posterio-lateral mar-
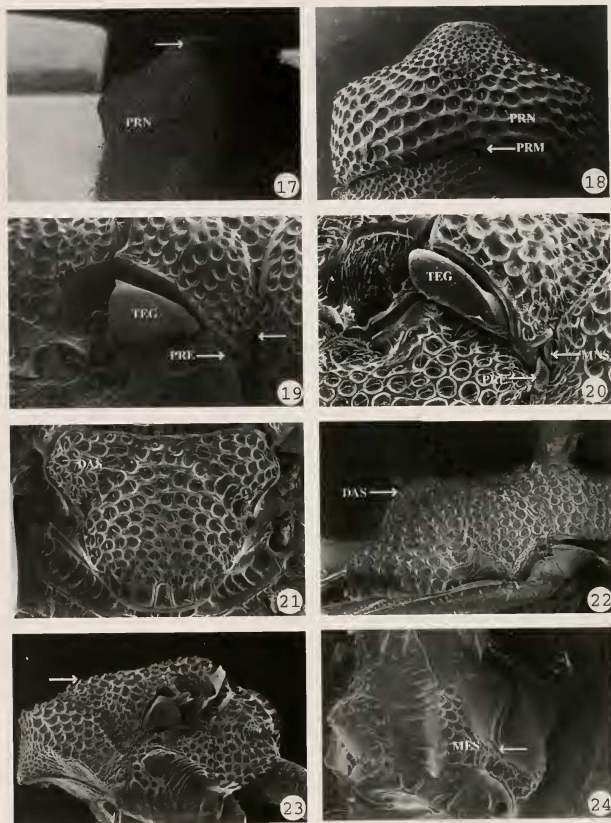
Figs. 17–24. 17–18. Pronotum (arrows indicate raised areas). 17. *Trigonura* sp. 18. *Phasgonophora sulcata*. 19–20. Mesothorax lateral view. 19. *Phasgonophora sulcata*. 20. *Cratocentrus* sp. 21–22. Axillae and scutellum. 21. *Phasgonophora sulcata*, 22. *Megachalcis* sp., 23. *Phasgonophora sulcata*, lateral view of the thorax (arrow indicate the sculpture). 24. *Chalcis* sp., mesepisternum.

gin. In Phasgonophorini and Barachymeriini the tegula is ventrally expanded giving a triangular appearance.

18. Dorsal axillar surface
   0. Flat (Fig. 21).
   1. Raised (Fig. 22).

The axillar carina divides the axilla into two regions, the lateral axillar surface and the dorsal axillar surface (Gibson 1985). Usually the dorsal axillar surface is flat and level with the scutum and scutellum. However in some Cratocentrini this surface is distinctly raised.

19. Sculpture of the mesosoma
   0. Not scabrous.
   1. Scabrous (Fig. 23).

It is difficult to define the surface sculpture of most chalcidoids. Within Chalcididae, Cratocentrini and Phasgonophorini have a sculpture much coarser than other chalcidids. Boucek (1992) referred to the sculpture of *Stypiura* as "rasp-like" and the sculpture of *Parastypiura* as "sharp transverse rugae". I divided the type of sculpture into two main groups: rasp-like and non rasp-like. The non rasp-like condition consists of many different sculptures that can not be grouped into distinct categories. Rasp-like sculpture consists of rough sharp projections or wrinkles and can be classified as scabrous (Harris 1979).

20. Mesepisternum
   0. Not projected between forecoxa (Figs. 24, 25).
   1. Projected medially between forecoxa (Fig. 26).

The mesepisternal region of Chalcididae is divided into two parts by a transverse carina. This carina delimits a smooth and angulate anterior mesepisternum from a horizontally sculptured ventral area anterior to the mid coxal foramen. Delvare (1992) called this sculptured ventral area the mesosternal shelf. The smooth area anterior to the carina has sometimes been referred to as the epicne-

mium and the carina as the epicnemial carina (Delvare 1992; Gibson 1985). The smooth epicnemial area supports the forecoxa. In some Cratocentrini the mesosternal shelf is anteriorly projected between the forecoxa (Fig. 26). The condition in other Chalcididae varies but the mesepisternum does not distinctly project as in some cratocentrines.

21*. Propodeum
   0. Angulate in relation to scutellum (Fig. 27).
   1. Horizontal in relation to the scutellum.
   2. Medially depressed and vertical with lateral projections (Fig. 28).
   3. Horizontal anteriorly and sloping steeply posteriorly (Fig. 29).

Characteristics of the propodeum have been used in classification of Chalcididae (Boucek & Delvare 1992). In most studies, however, the arrangement of carinae on the propodeum has been given more importance than the overall structure. These patterns of carina are autapomorphic and do not indicate relationships among the genera. Within Chalcididae the propodeum of Cratocentrini is unique, being medially short (depressed) and vertical between the lateral angulate projections (Fig. 28). In many Phasgonophorini species the propodeum has the anterior ⅓–⅔ horizontal and steeply sloping posteriorly. A steeply sloping posterior portion of the propodeum is a unique feature of the tribe. However there are variations within the tribe. For example, in *Stenochalcis* the propodeum is almost parallel to the scutellum although closer examination shows that more than ⅔ of the anterior propodeum is parallel to the scutellum and the posterior ⅓ is steeply sloping as in other Phasgonophorini. The posteriorly sloping propodeum is not very prominent in *Trigonurella* where the propodeum seems angulate. Comparative study shows that it is a variation of the sloping
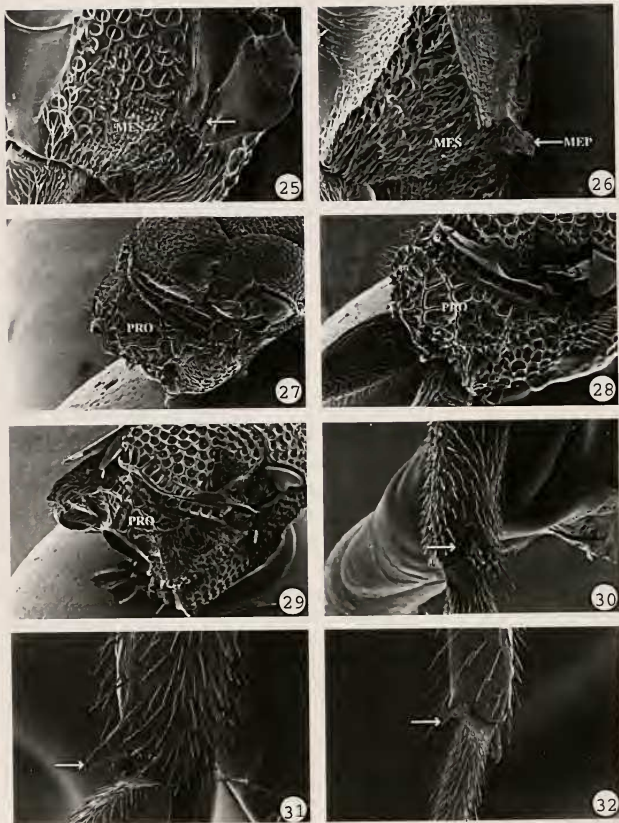
Figs. 25–32.   25–26. Mesepisternum. 25. *Phasgonophora sulcata*. 26. *Cratocentrus* sp. 27–29. Propodeum. 27. *Brachymeria* sp. 28. *Phasgonophora sulcata*. 29. *Cratocentrus* sp. 30–32. Foretibiae apex (apex indicated by arrow). 30. *Brachymeria* sp. 31. *Cratocentrus* sp. 32. *Phasgonophora sulcata*.

propodeum and not similar to the angulate state in other chalcidids.

Characters of the Legs:

22*. Apical margin of the foretibia.
    0. Without horizontally directed stout spur or elongation (Fig. 30).
    1. With horizontally directed stout spur (Fig. 31).
    2. Without horizontally directed spur but distinctly expanded giving the appearance of a spur (Fig. 32).
    In Cratocentrini there is a distinct short outward directed spur at the apex of the foretibia. This is in addition to the usually long, modified spur that forms the antennal brush (strigil). Other chalcidids do not possess such a spur but in Phasgonophorini the apex of the foretibia has expanded outwards, giving the appearance of a horizontal spur.

23. Shape of the hindcoxa.
    0. Elongate, more than 2× as long as broad (Fig. 33).
    1. Not elongate, 2× as long as broad or less (Fig. 34).
    A greatly swollen hind coxa is characteristic of all species of Chalcididae. The hindcoxa of many chalcidoids is swollen proximally and are pear-shaped or club-shaped. However the shape and size of the hindcoxa varies among different groups within the Chalcididae. Brachymeriini and Haltichellinae usually have a short pear-shaped hindcoxa whereas Chalcidini has a long club-shaped hindcoxa. Although many taxa of Cratocentrini and Phasgonophorini have long club-shaped hindcoxa as in other chalcidines, a few taxa in both groups exhibit the pear-shaped hindcoxa.

24. Inner basal tooth of the hindfemur.
    0. Absent (Fig. 35).
    1. Present (Fig. 36).
    On the hindleg near the articulation of the trochanter and femur in Chalcididae, where the arched tibia fits into the dentate margin of the femur, some species possess a distinct tooth, which originates from the inner side of the femur. This tooth makes a furrow or notch into which the hind tibia can be folded. This character has been used for identification of the genera of Cratocentrini (Boucek 1988), but it has not been used for determining phylogenetic relations. The inner tooth is present in many cratocentrines but is not found among the phasgonophorines.

25. Length of the hindtibia.
    0. Short, not reaching the trochanter (Fig. 37).
    1. Long, touching the trochanter (Fig. 38).
    The hindtibia is arched and fits into the toothed margin of the femur in almost all Chalcididae although the degree of curvature of the tibia varies among groups. The curvature of the tibia has been used as a character in chalcidid taxonomy, the length of the hind tibia has never been used. Usually, in the folded position, the hindtibia touches the trochanter near its point of articulation to the femur but in some groups the tibia is distinctly shorter and terminates before reaching the trochanter. This feature occurs only in chalcidids with a diagonally truncated hind tibial apex. Haltichellinae have a perpendicularly truncated hindtibial apex, but the tibia is not distinctly arched.

26. Tarsal depression of hind tibia.
    0. As long as first tarsal segment (Fig. 39).
    1. As long as first two or three tarsal segments combined (Fig. 40).
    2. Longer than first three tarsal segments combined (Fig. 41).
    The tarsal depression refers to the dorsal area of the hindtibia, which accommodates the tarsus when folded. In Chalcididae a distinct tarsal depression is not frequently observed except in a few groups. Groups that possess a distinct tarsal depression include Epitraninae and Cratocentrini. Within the groups that
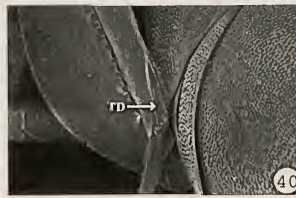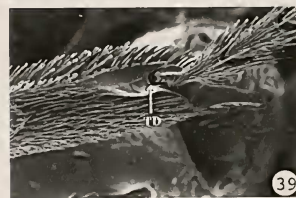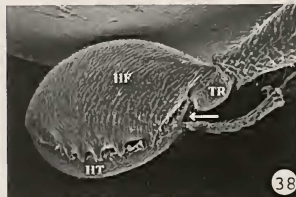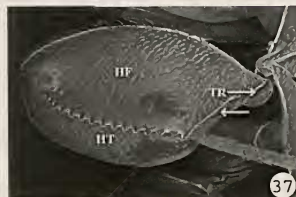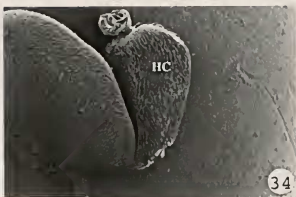
Figs. 33–40. 33–34. Hind coxa and femur. 33. *Cratocentrus* sp. 34. *Megachalcis* sp. 35. *Phasgonophora sulcata*, inner surface of hind femur. 36–38. Hind femur and tibia. 36. *Cratocentrus* sp. (inner surface). 37. *Trigonura* sp. 38. *Cratocentrus* sp. (outer surface). 39–40. Tarsal depression. 39. *Stypiura* sp. 40. *Vespomorpha* sp.

show a tarsal depression the length of this depression may vary. I divided this variation into the above three states.

27. Hind tibial spurs.
    0. Absent.
    1. Single stout spur present (Fig. 42).
    2. Single weak spur present (Fig. 43).

The number of hind tibial spurs has been used to characterize various family groups and genera of Chalcididae (Boucek 1992). The subfamily Chalcidinae characteristically has only a single hind tibial spur or none. Boucek (1992) stated that Cratocentrini and Phasgonophorini do not possess hind tibial spurs. My studies revealed that many phasgonophorine genera have a single hind tibial spur that is very reduced in size (Fig. 42). Chalcidini and Brachymeriini also have a single hind tibial spur, but it is well developed and appears flexible and weak relative to the stout spur found in Phasgonophorini.

28*. Apex of the hindtibia.
    0. Diagonally truncate, ventral corner at acute angle but not produced into a spine (Fig. 37).
    1. Diagonally truncated, elongated into a spine (Fig. 38).

The tip of the hindtibia of Chalcididae shows three different states: truncated at a right angle, diagonally truncated and elongate into a long spine, or diagonally truncated but not elongate into a spine. In Chalcidini, Cratocentrini, Dirhininae, and Epitraninae the hindtibial apex is elongate into a spine. In all Brachymeriini and Phasgonophorini it is diagonally truncated but not elongated into a spine.

Characteristics of the Wings:

29*. Patch of elongate setae on the anterior ventral margin of the forewing.
    0. Absent.
    1. Present (Fig. 44).

Species of Cratocentrini have a patch of posteriorly directed elongate setae on the ventral surface of the forewing near the distal end of the costal cell. This is an autapomorphy for the tribe.

30. Hamuli.
    0. Proximal hamulus straight, not curved like others, and separated slightly (less than its own length) from the others (Fig. 45).
    1. Proximal hamulus straight and distinctly separated (at least by a distance equal to its own length) from the others (Fig. 46).
    2. Three hamuli morphologically similar and located equidistant from each other (Fig. 47).

The hamuli are structures on the anterior margin of the hindwing used for wing coupling. Most chalcidids have three hamuli on each hindwing, although the number varies, especially in Epitraninae. The proximal hamulus is not curved as the others and could not function for coupling. The two hamuli distal to the body do the coupling of wings and the one proximal to the body probably has more of a sensory function. Since it is not curved it looks different from the other hamuli. It is also separated slightly from the two distal hamuli. However in Cratocentrini the proximal hamulus is not differentiated from the other two. It is curved and located equidistant from the distal hamuli. In *Brachymeria* the straight proximal hamulus is separated distinctly from the distal pair (Fig. 46); this is autapomorphic for the genus.

31. Length of postmarginal vein.
    0. Shorter than marginal vein (Fig. 62).
    1. Longer than marginal vein (Fig. 63).
    2. As long as marginal vein (Fig. 64).

Wing venation has been used by many chalcidoid taxonomists to define and identify genera (Boucek 1988; Delvare 1992). Grissell (1995) unsuccessfully attempted to quantify wing venation based on vein length ratios, and Heydon (1989) hypothesized that primitive pteromalids

Figs. 41–48. 41. *Cratocentrus* sp., tarsal depression. 42–43. Hind tibial spur. 42. *Stypiura* sp. 43. *Brachymeria* sp. 44. *Cratocentrus* sp., anterior ventral margin of the forewing. 45–47. Hamuli. 45. *Phasgonophora sulcata*. 46. *Brachymeria* sp. 47. *Cratocentrus* sp. 48. *Chalcis* sp., petiole.

have a postmarginal vein longer than the marginal vein. However the length of the postmarginal vein varies within chalcidids. The shorter postmarginal (than marginal) characteristic of Phasgonophorini and Brachymeriini is almost equal in length to the stigmal vein in Phasgonophorini and longer than the stigmal vein in Brachymeriini. Cratocentrini and *Chalcis* have a longer postmarginal vein, much longer than the stigmal vein and as long as or longer than the marginal vein.

32. Length of marginal vein relative to stigmal vein.

    0. More than four times the length of stigmal vein (Fig. 62).

    1. Less than four times the length of stigmal vein (Fig. 63).

Cratocentrini have a distinctly shorter marginal vein than most other chalcidids. In most chalcidids the marginal vein is more than four times the length of the stigmal vein.

Characteristics of the Metasoma:

33. Petiole length.

    0. Longer than wide (Fig. 48).

    1. Transverse, not visible in dorsal view (short) (Fig. 49).

    2. Half as long as wide; visible in dorsal view (Fig. 50).

The attachment of the petiole to the metasoma is characteristic of different groups of chalcidids but the size of the body of the petiole varies within groups. In many groups, the petiole varies from transverse to distinctly long and slender, although in some groups (e.g. Cratocentrini) it is constant in size. The surface of the petiole is sometimes differently sculptured in various groups, and this may be phylogenetically informative at the species level. In Cratocentrini, the petiole is transverse and not visible in dorsal view, whereas in phasgonophorini the petiole varies from transverse and not visible in dorsal view (usual condition) to half as

long as wide and visible in dorsal view (rarely).

34. Lateral sulcus of first metasomal tergum.

    0. Absent (Fig. 51).

    1. Present (52).

In *Phasgonophora*, the anterior dorsal area of the first tergum is raised into a transverse crest followed by longitudinal carinae (Fig. 52). These carinae are laterally delimited by a sulcus, which originates near the petiole and runs along the dorsolateral margin of tergum one, ending before the posterior margin of the tergum. A similar sulcus is present in some other Phasgonophorini. The transverse crest is autapomorphic for *Phasgonophora*.

35. First and second metasomal terga of females.

    0. Independent (Fig. 52).

    1. Fused, line of fusion distinct (Fig 51).

    2. Fused, no trace of line of fusion (Fig. 53).

The structure of the basal terga varies in chalcidids. Some species of Phasgonophorini have the first two basal tergites fused, without a trace of the line of fusion, so that only six terga are visible. In other Phasgonophorini, the two terga may be independent, the second tergite anteriorly telescoped into the first or united with the fusion line apparent, so that it is possible to count seven metasomal segments. Steffan (1959) suggested that the enlargement of the first tergites of Phasgonophorini gives rigidity for the abdomen for drilling in wood and attacking xylophagous beetle larvae.

36. Fifth metasomal tergum of the female.

    0. As long as the first tergum (Fig. 53).

    1. Distinctly shorter than the first tergum (Fig. 52).

In many chalcidids the tergum 1 is subequal in length to the preceding terga but in a few chalcidids the tergum 5 is longer and covers a major part of the metasoma. In Cratocentrini tergites 2–4 are almost hidden under tergum 1 and the ter-
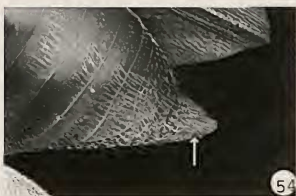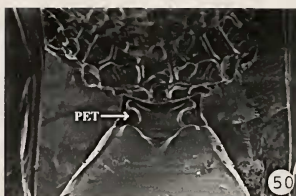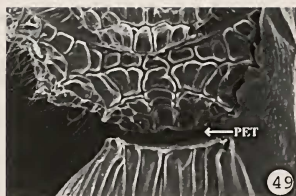
Figs. 49–56. 49–50. Petioles. 49. *Phasgonophora sulcata*. 50. *Stypiura* sp. 51–53. Metasoma. 51. *Stypiura* sp. 52. *Phasgonophora sulcata*. 53. *Cratocentrus* sp. 54–56. VIIth abdominal tergite and ovipositor (arrows indicate the VIIth tergum). 54. *Trigonurella* sp. 55. *Phasgonophora sulcata*. 56. *Cratocentrus* sp.

gum 5 is almost as long as the tergum 1 (Fig. 53). Reduction of terga 2–4 gives rigidity to the abdomen of Cratocentrini for drilling in wood (Steffan 1959).

37. Lengths of the seventh metasomal tergum and ovipositor sheaths.
    0. Not elongate, completely covering the short ovipositor sheath (Fig. 54).
    1. Elongate, completely covering the long ovipositor sheaths (Fig. 55).
    2. Short, not covering the elongate ovipositor sheaths (Fig. 56).
    3. Slightly elongate, covering the ovipositor sheaths (Fig. 65).

Cratocentrini are unique in having distinctly elongate ovipositor sheaths that are exposed beyond the apex of the metasoma (Fig. 56). It is also characteristic of most Phasgonophorini to have elongated ovipositor sheaths but in this case they are not exposed, and instead the seventh metasomal tergite has also been elongated to cover the sheaths. Elongation of the seventh metasomal segment (which is correlated with the elongation of ovipositor) can be observed in some species of *Brachymeria* and also in Haltichellinae (Fig. 56). However, these two conditions are not homologous. In the case of Haltichellinae and *Brachymeria*, the tergite is produced beyond the location of cerci. Hence the cerci are located closer to the anterior margin of the eighth tergite.

In Phasgonophorini, the anterior part of the tergite is produced. This is evident by the position of cerci. In Phasgonophorini the cerci are located closer to the posterior margin of the seventh metasomal tergite. The seventh tergite in *Trigonurella* is short, completely covering the ovipositor sheath as in the majority of *Brachymeria*. In the *Stenochalcis* the seventh tergite is intermediate between *Brachymeria* and many Phasgonophorini. However the state in *Stenochalcis* is homologous to other Phasgonophorini because the cerci are located closer to the posterior margin of tergite seven.

38. Density of the setae on seventh tergite.
    0. Uniformly distributed (Fig. 57).
    1. Densely distributed beyond cerci (Fig. 58).

This is a character that varies within the tribe Phasgonophorini. In some species the surface area beyond the cerci is distinctly different from the anterior part of the seventh tergite. The difference seems to be in the density of hairs, the posterior region having more dense hairs (Fig. 58).

39. Tufts of silvery setae on metasomal tergites (Fig. 53).
    0. Absent.
    1. One pair of lateral tufts on tergite five.
    2. Two pairs of lateral tufts on tergite five and six.
    3. Single continuous tuft on tergite five.
    4. Silvery hairs evenly distributed on all tergites.

Silvery setae on metasomal tergites are characteristic of Cratocentrini. I have identified four different patterns. *Acanthochalcis* and *Cratocentrus* have two pairs of lateral tufts on their fifth metasomal tergite whereas *Acrocentrus* and *Spatocentrus* have a single pair. Steffan (1959) suggested that these silvery setae patterns provide good characters for identification of Cratocentrini.

40. Posterior end of ovipositor sheath.
    0. Straight (Figs. 55, 56).
    1. Curved downwards (Fig. 59).

Both Phasgonophorini and Cratocentrini have distinctly elongate ovipositor sheaths. Cratocentrini have completely exposed sheaths because the last metasomal tergite is short and in Phasgonophorini most of the sheath is covered by the elongate seventh tergite. In general the sheaths are straight but in some groups of Phasgonophorini the sheaths are distinctly curved downward.

Figs. 57–59. 57–58. VIIᵗʰ tergum. 57. *Phasgonophora sulcata.* 58. *Stypiura* sp. (arrow indicate are of different sculpture). 59. *Stypiura* sp., VIIᵗʰ tergum and ovipositor (arrow indicates the ovipositor).

Phylogenetic Analysis

The branch and bound search option of PAUP yielded 14 most parsimonious completely resolved trees of length 98, consistency index of 0.646, and retention index of 0.843. The strict consensus tree (Fig. 66) shows that the 14 trees were a result of only three areas of conflict. The first conflict (I in Fig. 66) involves the placement of one outgroup (*Dirhinus*), whereas the second and third conflicts (II & III in Fig. 66) involve the Cratocentrini clade. The cladogram with the best character evidence was selected by using successive character weighting (Carpenter 1988). Reanalysis after successive weighting using the retention index and a base weight of 1000 yielded a single most parsimonious tree with a consistency index of 0.826 and retention index of 0.940 (Fig. 67), which is 98 steps long under equally weighted characters.

Selection of outgroup taxa could affect the relationships among the genera within Phasgonophorini and Cratocentrini. To test the effect of my outgroups on relationships among ingroup taxa I ran the analysis deleting one outgroup at a time. The three analyses gave ingroup tree topologies identical to that observed with all three outgroups. This indicates that there is no effect of the selected outgroups on intra-tribal relationships proposed in this study. The outgroups *Brachymeria* and *Dirhinus* form a monophyletic group with Phasgonophorini, to the exclusion of Cratocentrini in all 14 most parsimonious trees. This supports my previous finding that Cratocentrini and Phasgonophorini together do not form a monophyletic group.

DISCUSSION

The first area of irresolution in the strict consensus (node I Fig. 66), accounts for seven of the most parsimonious trees, by alternating the placement of *Dirhinus*. In one set of seven most parsimonious
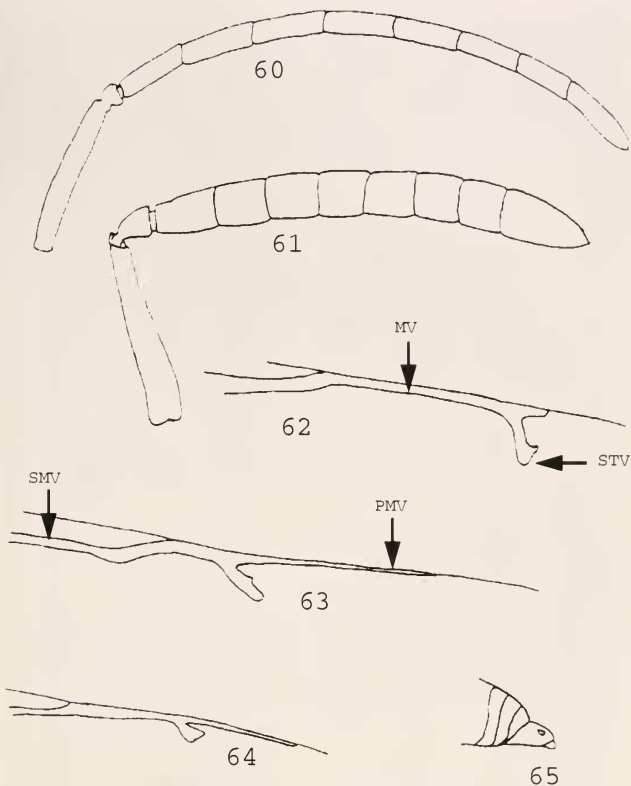
Figs. 60–65. 60–61. Antennae. 60. *Phasgonophora sulcata* 61. *Cratocentrus* sp. 62–65. Forewing venation. 62. *Phasgonophora sulcata.* 63. *Cratocentrus* sp. 64. *Chalcis* sp. 65. *Stenochalcis* sp., VIIth tergum and ovipositor.

trees *Dirhinus* is placed as sister to Phasgonophorini + *Brachymeria* while in the other set of seven trees with an otherwise identical topology, *Dirhinus* is placed as the sister group to Phasgonophorini (Fig.

68, A & B). The second area of conflict (node **II** Fig. 66), which involves the relationship between *Acanthochalcis* and *Megachalcis*, also has two posibilities (Fig. 69, A–F vs. G). The third area (node **III** Fig.
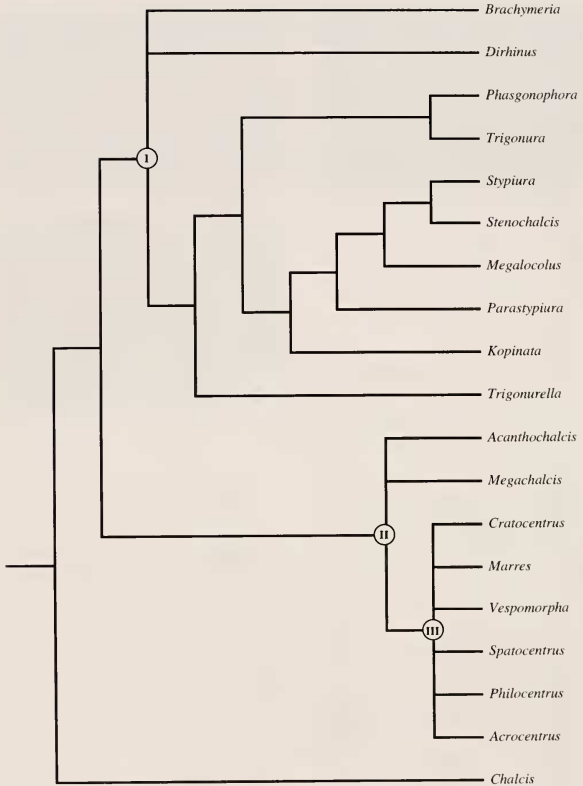
Fig. 66. Strict consensus cladogram of the 14 minimal length trees that resulted from the parsimony analysis of the character data in Table 1 (Length = 98, consistency index = 0.643, retention index = 0.843).

66), involves all the Cratocentrini except *Acanthochalcis* and *Megachalcis,* and has seven posibilities (Fig. 69, A–G). In four of the seven resolutions *Acrocentrus, Philocen-* *trus* and *Spatocentrus* form a clade within Cratocentrini with *Acrocentrus* being the sister group of the other two taxa (*Acrocentrus* clade) (Fig. 69, C–F). In two of

these four resolutions the *Marres* + *Vespomorpha* clade alternates from being the sister group of the *Acrocentrus* clade to being the sister group of a more inclusive *Cratocentrus* + *Acrocentrus* clade (Fig. 69, C & D). In the other two resolutions, (Fig. 69, E & F) a paraphyletic *Marres* and *Vespomorpha* alternate being the sister group to the *Acrocentrus* clade while *Cratocentrus* remains the sister group to them. Both resolutions in which *Marres* or *Vespomorpha* become sister to the *Acrocentrus* clade have a zero length branch and hence are not fully supported by the data (Coddington & Scharff, 1994). Two of the remaining three resolutions (Fig. 69, B & G) have a monophyletic *Spatocentrus* + *Philocentrus* group, with the monophyletic *Cratocentrus* + *Acrocentrus* as the sister group in one resolution (Fig. 69, G) and *Marres* + *Vespomorpha* as the sister group in the other (Fig. 69, B). The third resolution (Fig. 69, A) is identical to the preferred hypothesis (after successive weighting). The characters that unambiguously support the different resolutions are indicated in Fig. 69, A–G.

Monophyly of Cratocentrini and Phasgonophorini

Monophyly of the tribes Cratocentrini and Phasgonophorini was supported in my previous analysis (Wijesekara 1997) of the higher level phylogeny of Chalcididae. However that analysis used only two taxa from each of these two tribes. The present analysis used all the known genera from both tribes and the results confirm the monophyly of both tribes. Monophyly is supported by twelve unambiguous characters in Cratocentrini and by five unambiguous characters in Phasgonophorini (Fig. 67). This study explicitly supports the monophyly of these tribes using character evidence for the first time. Steffan (1950b) defined Cratocentrini using the following characters: antenna inserted just above the clypeus (Character 5 of this study); forewing with postmarginal vein longer than

short marginal vein (Character 31); metafemur with an inner tooth basally (Character 24); metatibia with long tarsal depression (Character 20); and female metasoma with only four visible terga. The number of visible metasomal terga is correlated with the size of the fifth metasomal terga. I have used the size of the fifth metasomal segment as a character instead of number of visible tergites. This study indicates that, of the characters used by Steffan, only the long tarsal depression supports the monophyly of Cratocentrini. New synapomorphies for the group, unambiguous in this study, are: 1) size of the labrum (Character 1, state 1); 2) reduced area between toruli and clypeus (character 2, state 2); 3) dorsally interrupted foraminal cavity (Character 11, state 1); 4) exposed mesonotal spiracal (Character 16, state 1); 5) medially projected mesepisternum (Character 20, state 1); 6) medially depressed propodeum (Character 21, state 2); 7) horizontally directed spur of foretibial margin (Character 22, state 1); 8) distinct tuft of spines on the front ventral margin of the forewing near distal end of the costal cell (Character 29, state1); 9) morphologically similar hamuli (Character 30, state 2); 10) marginal vein less than 4× the length of stigmal vein (Character 32, state 1); and 11) short seventh metasomal tergite (Character 37, state 2).

The tribe Phasgonophorini was defined by the following characters (Steffan, 1950a): face convex (Character 4 in this study); occiput concave; clypeus located away from lower ocular margin (Character 5); pronotum long (Character 12); procoxae modified to receive mandibles; abdominal tergite VII of the female elongated (Character 37); and sculpture of the thorax consisting of large foveoles (Character 19). The concave occiput and modified procoxae are common to most chalcidids and hence I did not use them as characters in this study. Except for the convex face and elongate tergite VII, all other characters are variable among phas-
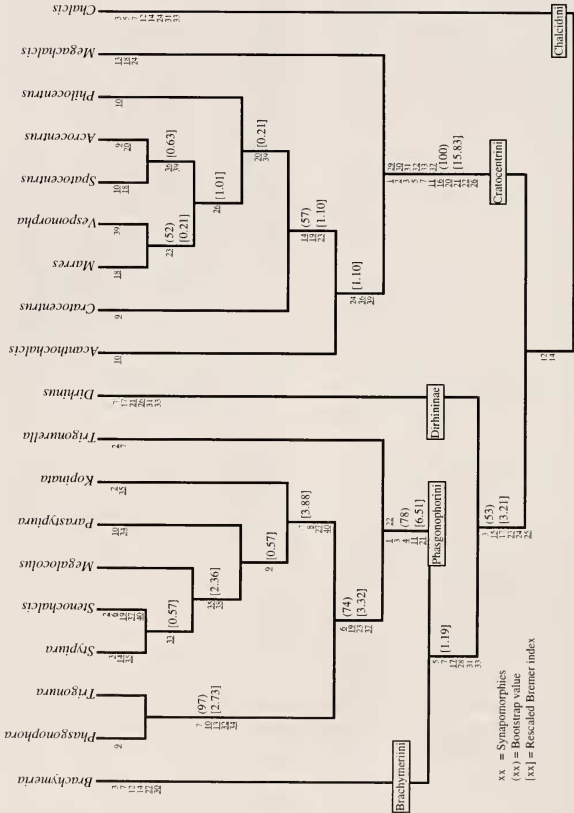
Fig. 67. Preferred most parsimonious tree for the data in Table 1 selected after successive weighting (Length = 98, consistency index = 0.823, retention index = 0.940).

xx = Synapomorphies
(xx) = Bootstrap value
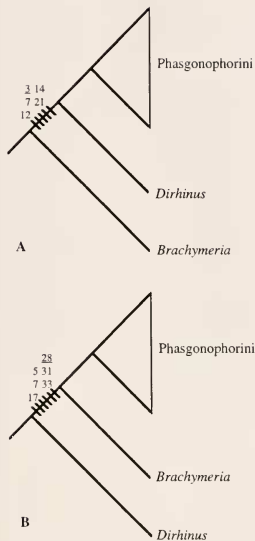[xx] = Rescaled Bremer index

Fig. 68. Two minimal length topologies which resulted from conflict I in strict consensus tree.

gonophorines. The present analysis indicates that only the convex face (Character 4, state 0) can support the monophyly of Phasgonophorini and provide the following new synapomorphies for the tribe: 1) labrum less than half as broad as base of mandible (Character 1, state 2); 2) dorsally interrupted foraminal cavity (Character 11, state 1); 3) posteriorly sloping propodeum (Character 21, state 3); and 4) expanded apical margin of the fore tibia (Character 22, state 2).

Boucek's suggestion that the tribes Phasgonophorini and Cratocentrini are closely related and probably sister groups is not supported by this analysis. The phylogenetic hypothesis suggested for groups

within Chalcididae from my previous analysis supports Brachymeriini as the sister group of Phasgonophorini. The present analysis corroborates this finding. Five synapomorphies support the sister group relationship between Phasgonophorini and Brachymeriini of which one character is unambiguous (Fig. 67): apex of hind tibia diagonally truncated, ventral corner at acute angle but not produced into a spine (Character 28, state 0). Other possible synapomorphies for the clade are: 1) antennal toruli located above the lower eye margin (Character 5, state 0); 2) short and triangular antennal depression with sharp margin (Character 7, state 3); 3) expanded tegulae (Character 17, state 1); and 4) petiole transverse (Character 33, state 1). Cratocentrini is the sister group of a clade that includes Brachymeriini and Phasgonophorini (Fig. 67). My analysis also suggests that *Trigonurella* is the sister group to the rest of Phasgonophorini and *Megachalcis* is the sister group to rest of the Cratocentrini.

Generic Relationships within Cratocentrini and Phasgonophorini

The generic relationships within Phasgonophorini are the same in all 14 most parsimonious cladograms which resulted from this analysis. Steffan (1950b) considered that Phasgonophorini had two distinct groups of genera. First, the *Phasgonophora* group with metasomal tergum 1 longer than tergum 2, and second, the *Stypiura* group with metasomal tergum 1 shorter than tergum 2. My analysis also provides support for these two groups. Each group is supported by four synapomorphies. The four unambiguous synapomorphies supporting the *Phasgonophora* group are: 1) presence of a carina behind lateral ocelli (Character 10, state 1); 2) pronotal surface raised lateral to the median line (Character 13, state 1); 3) marginal vein less than four times the length of stigmal vein (Character 32, state 1); and 4) presence of a lateral sulcus on first ab-
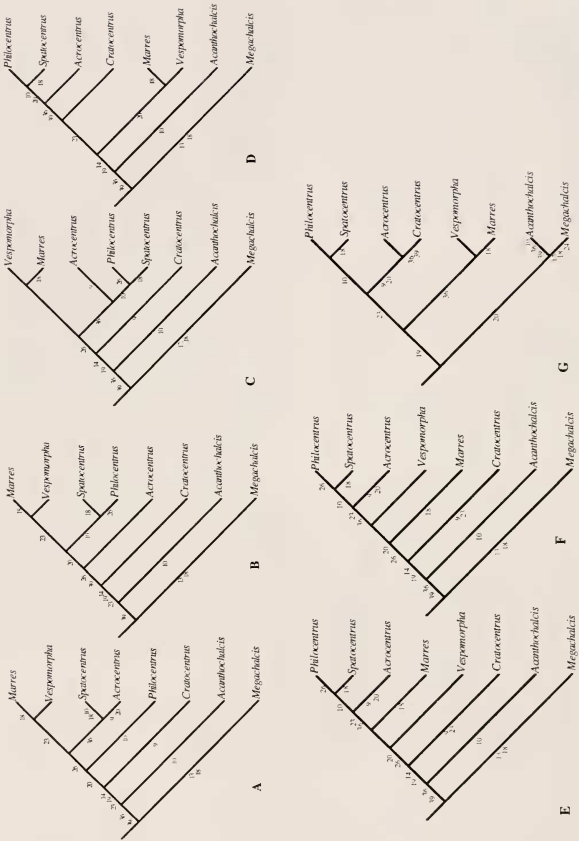
Fig. 69. Seven minimal length topologies which resulted from conflict III in strict consensus tree.

dominal tergite (Character 34, state 1). The synapomorphies supporting the *Stypiura* group are: 1) antennal scrobe short and triangular with a blunt margin (Character 7, state 1); 2) ocellar triangle raised above vertex (Character 8, state 1); 3) presence of a single stout spur on hind tibial apex (Character 27, state 1); and 4) downwards curved posterior end of ovipositor sheath (Character 40, state 1) (Fig. 2). Except for character 7, state 1, the others are unambiguous. In addition, this analysis suggests that *Trigonurella* forms a distinct third group within Phasgonophorini (Fig. 67).

Conflicting evidence from the characters evaluated gave seven equally parsimonious resolutions for generic relationships within Cratocentrini (Fig. 69, A–G). I have selected a single hypothesis of generic relationships using successive character weighting which best explains the characters used (Fig. 67). However, most Cratocentrini (except *Acanthochalcis* and *Cratocentrus*) are known from very few specimens. Therefore, we have limited knowledge of character variation within the tribe and the question of the value of some of the selected characters as evidence of phylogenetic affinities remains open.

Stability of the Phylogeny

Bootstrap analysis and rescaled decay indices indicate substantial support for most of the nodes in the selected phylogeny (Fig. 67). Within Phasgonophorini the two clades that agree with Steffan's groups have more than 50% bootstrap support while the clades within Cratocentrini have little bootstrap support. The rescaled branch support values are shown in Figure 67. The total support index (Bremer 1994) for the selected tree is 0.449.

Implications of the Tribal Analysis for the Phylogeny of Chalcididae

According to the family-level phylogenetic analysis of Chalcididae (Wijese-

kara 1997), neither Cratocentrini + Phasgonophorini nor Brachymeriini + Chalcidini are sister groups. The results of this analysis corroborate the results obtained from the family-level analysis. However, the results of generic level analysis within the tribes indicate that *Megachalcis* and *Trigonurella* are basal taxa within Cratocentrini and Phasgonophorini, respectively. When sampling taxa from a group for inclusion as exemplars in a phylogenetic analysis it is most appropriate to select representatives that are ancestral within the group, as it is more likely that their character states represent the ground plan. In my earlier analysis, I represented Cratocentrini by *Cratocentrus* and *Acanthochalcis*, and Phasgonophorini by *Phasgonophora* and *Megalocolus*. The two apparently most basal groups, *Megachalcis* and *Trigonurella*, were left out. To determine whether my taxon sampling had any effect on family-level phylogeny, I coded *Megachalcis* and *Trigonurella* for the 34 morphological characters used in the family phylogeny and reanalyzed the data. This analysis resulted in the same 42 most parsimonious trees with identical topologies to my previous analysis (Fig. 70) indicating that my results are not affected by taxon sampling.

Sampling of characters as well as sampling of taxa may affect the results of a phylogenetic analysis. The characters used depend on the taxon sample that is selected for the study. The characters that are informative at the lower level of phylogeny may not be suitable to study the relationships at a higher phylogenetic level, hence I have selected one character data set for the study of family phylogeny and a separate data set to study the generic relationships within the tribes (eight characters were common to both data sets). To test the effect of combining the two data sets I scored all the taxa for all the characters (Appendix 2) and reanalyzed the resulting data matrix of 41 taxa and 65 characters (Table 3). The
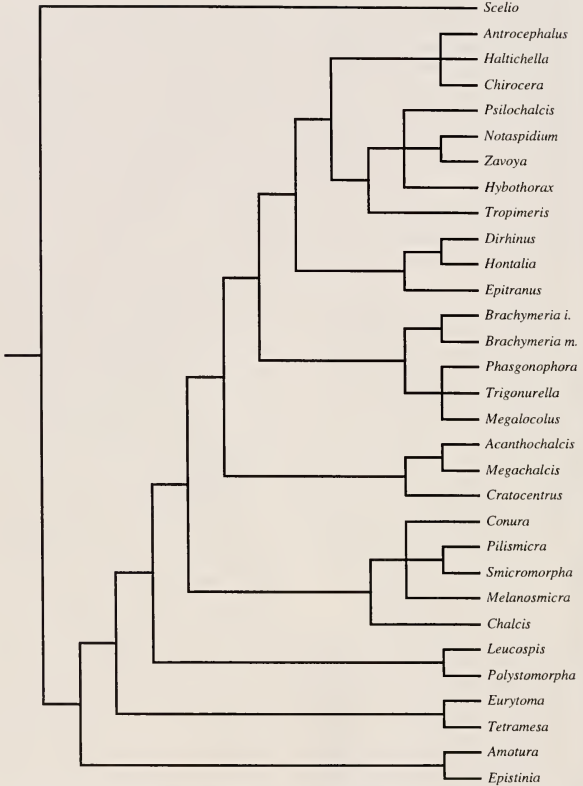
Fig. 70.   Phylogeny of Chalcididae. Single most parsimonious tree resulted from successive character weighting after inclusion of basal Phasgonophorini and Cratocentrini taxa (*Trigonurella* and *Megachalcis*) in the taxon sample of the previous study.

Table 3. Data matrix (combined character sets) (polymorphic characters: a = state 0 or 1, b = 0 or 2, c = 0 or 3, d = 1 or 3, e = 1 or 2).

```
                                        Characters

               1111111111 2222222222 3333333333 4444444444 5555555555 666666
Taxa  123456789 0123456789 0123456789 0123456789 0123456789 0123456789 012345

Scelio          000?10?20 00?10?20?0 ?00?10?00a 02?0?10?00 00000????0 0000?1??10 00??00
Leucospis       0?0?0??20 03001110?. ?112001000 0110?10000 11?0010000 0000110010 002000
Polystomorpha   0?0020040 0300111001 ?112001000 0110210000 1100010??0 0000110010 002000
Eurytoma        0?0000030 1401000000 ?010001000 0010200000 00000???0? 00000160a0 000000
Tetramesa       0005000?0 0401000000 ?010001000 0010200000 00000????0 00000160a0 0a0000
Amotura         010010020 1201017000 ?010000010 0001100000 1000000100 0000300010 000000
Epistenia       010010020 0201017000 ?010000000 0010000010 1100000??0 0000300010 003000
Antrocephalus   001110101 100b1a?000 0011110112 01a0000000 2100010?00 0000c12110 01c000
Haltichella     001110101 100b1a?000 0011110112 01a0000000 2100010?70 0000012110 01c000
Chirocera       001110101 100211?000 0011110112 0110000000 2100010??0 0000112110 010000
Psilochalcis    001210101 10021a?000 0011110112 0110200000 2100010?70 1000212110 010000
Notaspidium     001210101 1102117000 0011110112 1110200000 2100010?70 1000212110 010000
Hybothorax      001210101 1000107000 0011110112 0110200000 2100010?70 1000212110 010000
Zavoya          001210101 1?02117010 ?011110112 1400000000 2101010??1 0000202110 110000
Tropimeris      001310101 1000117000 0011110112 0510200000 2100010??0 1000212110 010000
Brachymeria i.  000400101 1202113000 0011120102 0100000000 2113110100 0110001112 011000
Brachymeria m.  000400101 1202113000 0011120102 0100000000 2113110100 0110001110 010000
Conura          100000101 1201111000 001d001102 0200000000 212300a000 00003030a0 010000
Pilismicra      100000101 0?01111000 ?013001100 0200200000 2113000170 000001?010 010000
Melanosmicra    100000101 12?1117000 0013001102 0200000000 2123001110 0003133000 010000
Chalcis         100000101 1201111000 0013001102 0200000000 2122001000 0000303000 010000
Smicromorpha    000000101 1001110000 0013031100 0300000000 2113000010 0002213000 000000
Dirhinus        000511101 11a0110000 0011110100 1110100000 2122010111 0000?050b0 010000
Hontalia        001511101 1110110100 ?011000100 1110100010 2122000111 0002050000 012000
Epitranus       013101101 11?011?000 0011110100 1110000000 22220001e1 0002004000 010000
Acanthochalcis  000010111 1422112001 1013001101 2110110001 2122001020 0021111210 002020
Megachalcis     000010111 1422112000 1013001101 2112111001 2122000020 0021111210 010020
Cratocentrus    000010111 1422112020 1013001101 2110210011 2122011020 0021111110 002020
Marres          000010111 1422112000 1013001101 2110211101 2122001010 0021111?10 002020
Vespomorpha     000010111 1422112000 1013001101 2110210101 2122001010 0021111210 002040
Spatocentrus    000010111 1422112001 1013001101 2110211101 2122011010 0021111110 012010
Philocentrus    000010111 1422112001 1013001101 2110210101 2122011020 0021111?10 0??0?0
Acrocentrus     000010111 1422112020 1013001101 2110210111 2122011010 0021111110 012010
Phasgonophora   000400121 1200000011 1011120101 3111100102 2112000100 0100011111 011000
Trigonura       000400121 1200000001 1011120101 3111100102 2112000100 0100011111 010000
Trigonurella    000400121 1210013000 1011120101 3110100002 2112010100 0100001110 010000
Stypiura        000400121 1201001110 1011120101 3110200102 2111000100 0100001220 111101
Megalocolus     000400121 1200001110 1011120101 3110100102 2111000100 0100001110 211101
Stenochalcis    000400121 1210011110 1011120101 3110100002 2111000100 0100001120 213100
Kopinata        000400121 1?10001100 1011120101 3110100102 2111000100 0100001210 111001
Parastypiura    000400121 1?00001111 1011120101 3110100102 2111000100 0100001111 011001
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polymorphic characters were scored as polymorphic using MacClade. PAUP's heuristic search with 500 random addition sequence replicates options gave 14 most parsimonious trees of length 234, consistency index of 0.491 and retention index of 0.818 (consensus tree Fig. 71).

Filtering trees to remove polytomous trees for which more highly resolved compatible trees exist, yielded 7 most parsimonious trees. Seven different resolutions resulted due to three areas of conflict (Fig. 71, A, B, & C). The first conflict (A) involves the placement of Smicromor-
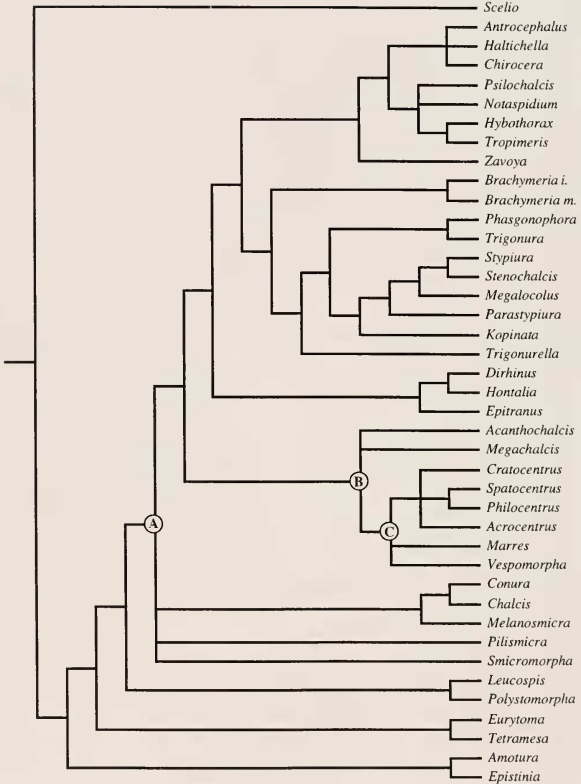
Fig. 71. Strict consensus cladogram of the 14 minimal length trees (Length = 234, consistency index = 0.491, retention index = 0.818) that resulted from the parsimony analysis of the character data in Table 3.

pha, the second conflict (B) involves the relationship between *Acanthochalcis* and *Megachalcis*, and the third conflict (C) involves the placement of *Marres* and *Ves-*

pomorpha. Successive weighting of the characters using the retention index and 1000 base weight gave 10 most parsimonious trees. Filtering the polytomous

trees yielded four most parsimonious trees (consensus tree Fig. 72). All 10 most parsimonious trees after successive weighting were 235 steps long under equal weighting of characters. Four most parsimonious trees after filtering resulted due to a single area of conflict indicated in the strict consensus tree (A in Fig. 72).

The joint character set favors somewhat different relationships within the family (see comparison in Fig. 73). To obtain the family phylogeny represented in the combined analysis from my previous data set requires two extra steps (tree length 101 instead of 99), and to get the previous family phylogeny from the combined data set requires seven extra steps (tree length 241 instead of 234).

The most obvious change is the shifting of Brachymeriini + Phasgonophorini lineage as the sister group of Haltichellinae instead of Dirhininae + Epitraninae clade. In addition, *Zavoya* becomes sister to the other Haltichellinae and *Smicromorpha* and *Philismicra* groups away from, instead of within, Chalcidini. The sister group relationship between Brachymeriini + Phasgonophorini and Haltichellinae is supported by six synapomorphies of which 3 are unambiguous [characters 29, 45, and 57 (Fig. 72)]. Of these, character 29 is from the family-level study, character 45 is from the tribe-level study and character 47 is common to both studies. None of these characters is unique and unreversed within the clade. In the family level phylogenetic study the sister group relationship between Haltichellinae and Dirhininae + Eipitraninae clade was also supported by six synapomorphies with only a single unambiguous character (Fig. 74). Of these characters, location of the antennal toruli remains a unique and unreversed synapomorphy for both clades while two other characters (Character 3 and Character 25) shows single reversals within the group. The other three characters are much more variable within the

group. Overall the six characters supporting Brachymeriinae + Epitraninae + Haltichellinae are less homoplasious (ci = 0.5, 0.7, 0.3, 0.5, 0.7, and 1.0 for characters 3, 4, 5, 11, 25, and 56 respectively) than the characters supporting the Haltichellinae + Brachymeriini + Phasgonophorini clade in combine analysis (ci = 0.5, 0.5, 0.5, 0.2, 0.2, and 0.4 for characters 16, 29, 42, 45, 48, and 57).

Similarly three synapomorphies (two unambiguous) support the Chalcidini clade including *Smicromorpha* in the family phylogenetic analysis (Fig. 74). The structure of the petiole (Character 56, state 3) is unique for the clade and characters 1 and 31 show a single reversal in *Smicromorpha*. In the combined character analysis, Chalcidini without *Smicromorpha* is supported by four characters (Fig. 72): 1) raised supra clypeal area (Character 1, state 1) and 2) longitudinally oriented spiracle (Character 31, state 2) from the family phylogeny data set; and 3) antennal scrobe shape (Character 16, state 1); and 4) longer postmarginal vein (Character 54, state 1); from the tribal data set. The diagonally truncated hind tibial apex (Character 42, state 1) and fifth metasomal segment (Character 61, state 0) separate *Smicromorpha* from other chalcidines (Fig. 72). The character set which support the Chalcidini + Smicromorphinae in family level study provide less support (ci = 0.5, 0.8, and 1.0 for characters 1, 39, and 56 respectively) than the character set supporting the Chalcidini excluding Smicromorphinae in combine analysis (ci = 1.0, 0.5, 0.8, 0.1, and 0.3 for characters 1, 16, 31, 32, and 34). The abdomen of *Smicromorpha* is highly modified and not comparable to any other chalcidids. Therefore it is highly unlikely that the length of the fifth metasomal segment in *Smicromorpha* can show phylogenetic affinities to other chalcidids. Hence character 61 should not be regarded as evidence for separating *Smicromorpha* from other chalcidines.
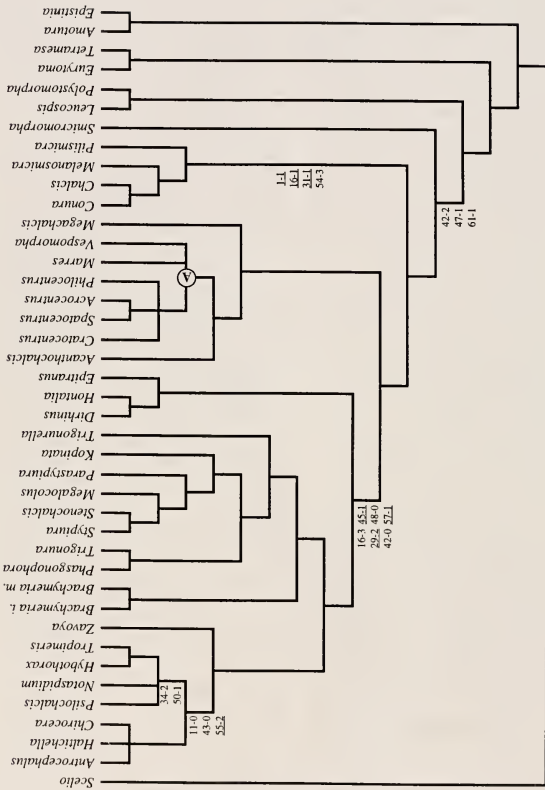
Fig. 72. Strict consensus cladogram of the 10 minimal length trees that resulted from the parsimony analysis of successively weighted data in Table 3 (Length under equal character weights = 235) (numbers on branches refers to character numbers in Appendix 2).
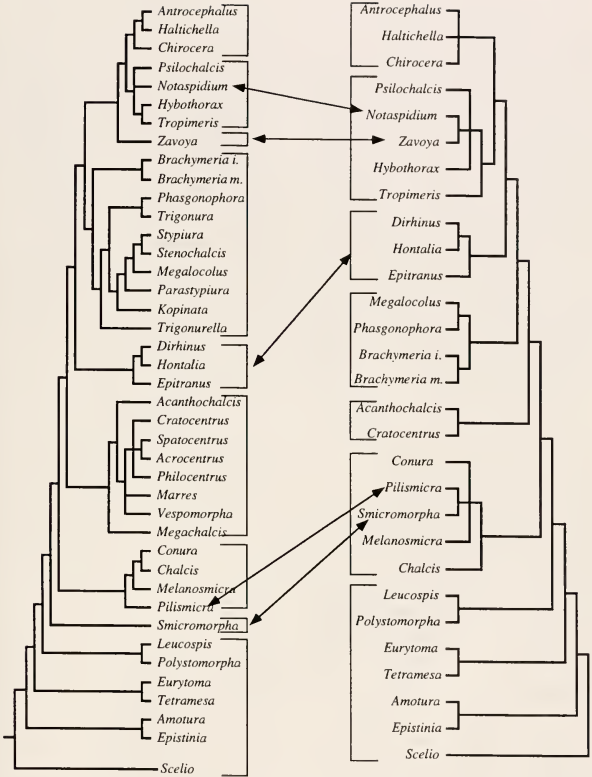
Fig. 73. Comparison of Chalcididae family cladograms resulted from my previous study and from combined character matrix in Table 3. Left. Consensus tree of 10 most parsimonious trees resulting from successive character weighting for combined data matrix. Right. Preferred family phylogeny from the previous study.

The third difference between the family study and the combined character analysis is that in the latter, *Zavoya* is placed as sister to all other Haltichellinae (Figs. 71, 72) instead of as sister to *Notaspidium* within Hybothoracini. (Fig. 74). Two ambiguous characters support the Hybothoracini + Tropimeridini clade (ex-
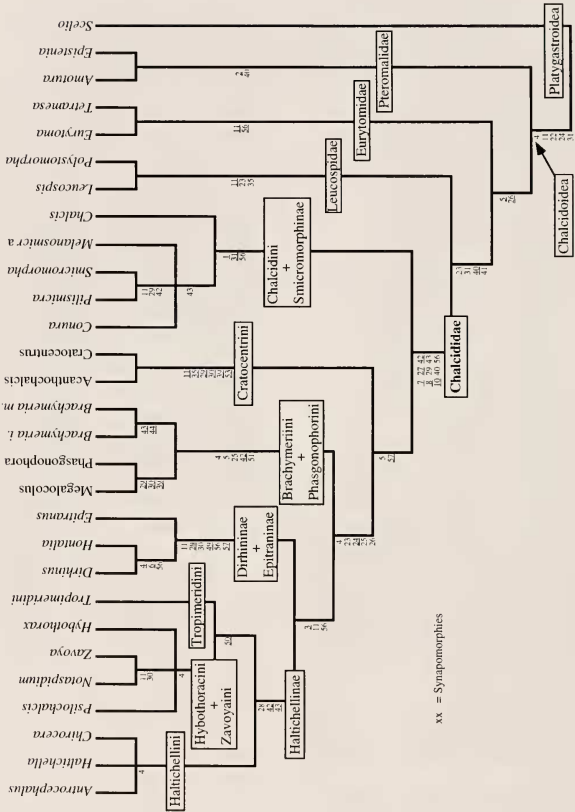
Fig. 74. The preferred family phylogeny of Chalcididae that resulted from my previous study indicating the synapomorphies for clades within the family (numbers on branches correspond to characters in Appendix 2).

xx = Synapomorphies

cluding *Zavoya*) in the combined analysis: the location of the postmarginal vein (Character 50, state 1), and the shape of posterior margin of the pronotum (Character 34, state 2). The sister group relationship between Haltichellini and Hybothoracini (including *Tropimeris*) is supported by three possible synapomorphies: 1) Hypostomal bridge (Character 11, state 3); 2) Presence of two hindtibial spurs (Character 43, state 1); and 3) Shorter marginal vein (Character 55, state 1). Only character 55 provides unambiguous support. Overall the Haltichellini +Hybothoracini including Zavoyini and Tropimeridini in family level analysis has support of less homoplasious characters (ci = 0.5, 0.6, and 0.5 for characters 28, 42, 43) than for Haltichellinae + Hybothoracini excluding Zavoyini in combined analysis (ci = 0.5, 0.4, and 0.2 for characters 11, 43, and 55).

These results clearly indicate that the characters used for analysis of generic relationships affected the resolution of higher level relationships. This means that the addition of characters which are homoplasious at higher phylogenetic level changed the evolutionary interpretation of characters used for resolving the higher level phylogeny.

It is obvious that combining two character sets that were selected by studying biased taxon samples in relation to one another will produce a data set with biased characters and a biased taxon sample. Therefore, the results of the combined analysis can not be regarded as an appropriate representation of phylogenetic relationships within Chalcididae. Although it is not appropriate to combine two data sets to make a biased data set, this exercise indicates that the family phylogeny I have suggested in my previous study should be subjected to more critical testing by including more taxa from different chalcidid groups to establish a stable phylogenetic hypothesis for the family.

ACKNOWLEDGMENTS

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APPENDIX 1: TAXA EXAMINED

Outgroups

1. *Brachymeria* spp.
2. *Chalcis* spp.
3. *Dirhinus* spp.

Cratocentrini

Acanthochalcis nigricans Cameron
Acanthochalcis unispinosa Girault
Acrocentrus erythrothorace Steffan
Cratocentrus ruficornis Cameron
Cratocentrus pruinosus Steffan
Marres dicomas Walker
Megachalcis carinata Steffan
Megachalcis hirticeps (Cameron)
Megachalcis malabarica Narendran
Megachalcis timerensis Boucek
Philocentrus argenteolus Steffan
Spatocentrus arnoldi Steffan
Vespomorpha auronitens Steffan

Phasgonophorini

Kopinata partirubra Boucek
Megalocolus ducator (Walker)
Megalocolus properator (Walker)
Megalocolus signator (Walker)
Megalocolus tentator (Walker)
Parastypiura pulchripennis (Ashmead)
Phasgonophora batesii Boucek
Phasgonophora gigentia Ashmead
Phasgonophora sulcata Westwood
Stenochalcis miltoni (Girault)
Stypiura candatus Guerin
Stypiura conuigastra (Perty)
Stypiura patesi (Kirby)
Stypiura rfiventris (Sichel)
Stypiura thoracica (Schel)
Trigonura algerti Burks
Trigonura bakeri Masi
Trigonura californica Rohwer
Trigonura dorsalis Ashmead
Trigonura elegans Provancher
Trigonura euthyrrhini Dodd
Trigonura indica Narendran
Trigonura insularis Cresson
Trigonura javensis Narendran
Trigonura leuzonensis Narendran
Trigonura pini Burks
Trigonura puertoricensis Wolcott
Trigonura radiator Walker
Trigonura samarensis Narendran
Trigonura steffani Narendran
Trigonura tarsata DellaTorre
Trigonura ulmi Burks
Trigonurella achterbergi Narendran
Trigonurella elegans Boucek

APPENDIX 2: CHARACTER DESCRIPTIONS (COMBINED SET)

The numbers within parentheses indicate the original data set that character came from (1= family level study and 2= tribel level study) and the character number in the original data set respectively.

Characteristics of the head:

1. Supraclypeal area (1/1).
    0. Not horizontally raised.
    1. Horizontally raised.
2. Distance between the antennal toruli (1/2).
    0. Distance not more than 2× the diameter of torulus.
    1. Distance more than 2× the diameter of torulus.
3. Orientation of the antennal toruli (1/3).
    0. Lateral and ventral margins of toruli produced forward.
    1. Lateral and ventral margins of toruli not produced and toruli facing forward or upwards.
4. Interantennal projection (1/4).
    0. Not modified; area between toruli continuous with face and appearing raised due to scrobal depressions.
    1. Modified into a round plate with blunt margins.
    2. Modified into a round plate with sharp elevated margins.
    3. Reduced to a thin sheet-like elevation between toruli.
    4. Modified into thick plate which is higher than upper toruli margin.
    5. Absent.
5. Location of the antennal toruli (1/5, 2/5).
    0. Toruli located at or above the level of the lower eye margin.
    1. Toruli located below the level of the lower eye margin.
6. Frons (1/6).
    0. Not produced into horns.
    1. Produced into two strong horns.
7. Labrum habitus (1/7).
    0. Base of the labrum covered by the anterior clypeal margin.
    1. Base of the labrum exposed, not covered by the clypeal margin.
8. Size of the Labrum (2/1).
    0. Large: as broad as base of the mandibles.
    1. Intermediate size: about half as long as base of mandibles.
    2. Small: less than half the length of base of the mandibles.
9. Base of the mandible (1/8).
    0. Covered by the genal margin.
    1. Exposed.
10. Postgenal carina (1/9).
    0. Absent.

1. Present.
11. Hypostomal bridge and genal bridge (1/10).
    0. Genal bridge absent, hypostomal bridge distinct, hypostomal carina continuous around occipital foramen.
    1. Genal bridge not complete, hypostomal carinae converge below occipital foramen making distinct hypostomal lobes which narrowly unite in the middle.
    2. Post gena converging below the occipital foramen; hypostomal bridge slightly exposed.
    3. Genal bridge absent, hypostomal bridge distinct, and hypostomal carina continuous with a distinct carina around occipital foramen.
    4. Genal bridge completely covering the hypostomal bridge.
12. Median area above clypeus and below antennal toruli (2/2).
    0. Same sculpture as rest of the face; not modified.
    1. Different sculpture; modified to form a bridge between toruli and clypeus.
    2. Absent.
13. Malar sulcus (2/3).
    0. Absent.
    1. Present as a sulcus.
    2. Indicated as a carina.
14. Face (2/4).
    0. Convex distinctly.
    1. Concave or flat.
15. Antennae (2/6).
    0. Slender and long.
    1. Stout and short.
16. Antennal scrobe (2/7).
    0. Long and parallel sided.
    1. Short and almost triangular with blunt margin.
    2. Long and triangular with sharp margin.
    3. Short and triangular with sharp margin.
17. Ocelli triangle (2/8).
    0. Ocelli close to each other and raised above vertex.
    1. Ocelli spread apart and triangle not raised.
18. Vertex within ocellar triangle (2/9).
    0. Normal not modified.
    1. Medially raised between lateral ocelli.
    2. Raised lateral to the lateral ocelli.
19. Carina behind lateral ocelli (2/10).
    0. Absent.
    1. Present.
20. Foraminal cavity/depression (2/11).
    0. Continuous around occipital foraman.
    1. Dorsally interrupted.

Characteristics of the mesosoma:

21. Notauli (1/11).
    0. Present.
    1. Absent.
22. Prepectus (1/12).

    0. Absent.

    1. Present.

23. Externally visible area of the prepectus (1/13, 2/15).

    0. Large and triangular sclerite; ventromedially broad.

    1. Small and distinctly longer than broad; ventromedially narrow, plate like (state 0 in 2/15).

    2. Reduced to a very thin sclerite difficult to see (state 1 in 2/15).

    3. Intermediate size sclerite, as long as broad; ventromedially narrow (state 2 in 1/13).

24. Mesopleural Wing Process (1/15).

    0. At least partly exposed.

    1. Completely covered by tegula.

25. Relative size and shape of the tegula (1/16, 2/17).

    0. Elongated and small, second axilla of the wing joint completely exposed.

    1. Both ventrally and posteriorly expanded, oval shape, second axilla completely covered.

    2. Ventrally expanded, second axilla of the wing exposed (state 1 in 2/17).

    3. Reduced and axilla exposed.

26. Orientation of the area between lower margin of the femoral depression and epicnemial carina in relation to sagittal plane (1/17).

    0. Parallel.

    1. Perpendicular.

27. Parascutal and axillar carinae (1/18).

    0. Converge but extend towards dorsum before meeting each other at transscutal articulation.

    1. Converge to meet each other at transscutal articulation.

28. Axillular carina (1/19).

    0. Absent.

    1. Present.

29. Frenal area of the scutellum (1/20).

    0. Not marked.

    1. Slightly marked.

    2. Distinctly marked by a lamina.

30. Propodeum (1/21, 2/21).

    0. Angulate in relation to scutellum.

    1. Horizontal in relation to scutellum.

    2. Anteriorly horizontal and steeply sloping posteriorly (state 2 in 2/21).

    3. Medially depressed and almost vertical (state 1 in 2/21).

31. Spiracle of the propodeum (1/22).

    0. Small and rounded.

    1. Spiracle elongated and transversely or obliquely oriented.

    2. Longitudinally oriented.

    3. Reduced.

    4. Sunken into propodeum.

    5. Lateral margin modified to a lamina which characteristically extends posteriad.

32. Width of the pronotum (2/12).

    0. Broad.

    1. Narrow anterior.

33. Pronotal surface (2/13).

    0. Not raised; normal.

    1. Raised lateral to the median line.

    2. Raised as two bumps near posterior lateral margin.

34. Posterior margin of the pronotum (2/14).

    0. Broadly concave.

    1. Medially acutly emarginate.

    2. Medially abruptly concave.

35. Mesonotal spiracle (1/14, 2/16).

    0. Covered by posterior lateral margin of pronotum.

    1. Exposed.

36. Dorsal axillar surface (2/18).

    0. Flat.

    1. Raised.

37. Sculpture of the mesosoma (2/19).

    0. Not rasp like.

    1. Rasp like.

38. Mesoepisternum (2/20).

    0. Not projected between fore coxa.

    1. Projected medially between fore coxa.

39. Apical margin of the fore tibia (1/23, 2/22).

    0. Without horizontally directed stout spine.

    1. With horizontally directed stout spine .

    2. Without a spur but distinctly expanded similar to spur .

40. Hind coxa (1/24).

    0. Not distinctly enlarged.

    1. Enlarged with flat inner surface.

    2. Enlarged with convex inner surface.

41. Hind femur (1/25).

    0. Normal (not enlarged and toothed).

    1. Enlarged and toothed.

42. Apex of the hind tibia (1/26).

    0. Truncate at right angle.

    1. Diagonally truncated ventral corner at acute angle but not produced into a spine.

    2. Diagonally truncated and elongated into a spine.

    3. Diagonally truncated and outer spur incorporated into a spine.

43. Hind tibial spurs (1/27, 2/27).

    0. Two spurs present.

    1. Single stout spur present.

    2. Spurs absent.

    3. Single weak spur present (state 1 in 2/41).

44. Elongated tooth-like process on hind tibial claws (1/28).

    0. Absent.

    1. Present.

45. Shape of the hind coxa (2/23).

    0. Proximally swollen but not elongated.

    1. Proximally swollen and elongated.

46. Inner tooth of the hind femur (2/24).

    0. Absent.

    1. Present.

47. Length of the arched hind tibia (2/25).
   0. Shorter than trochantus -femoral joint.
   1. Tip of the tibia touching the trochantus-femoral joint.
48. Tarsal depression of hind tibia (2/26).
   0. As long as first tarsal segment.
   1. As long as first two or three tarsal segments together.
   2. Longer than first three tarsal segments together.

Characteristics of the wings:

49. Length of marginal vein in relation to submarginal vein (1/30).
   0. Marginal vein short, submarginal vein less than half the length of submarginal vein.
   1. Marginal vein as long as submarginal vein, if shorter submarginal vein not 2× longer than marginal vein.
50. Forewing marginal vein location (1/31).
   0. Located at the anterior margin of the forewing; postmarginal and stigmal veins well developed.
   1. Located away from the anterior margin; post marginal and stigmal veins rudimentary.
51. Vertical nebulous vein on hind wing (1/32).
   0. Absent.
   1. Present.
52. Hamuli (2/30).
   0. Hamulus proximal to body different from others and located slightly away from the rest (less than its own length).
   1. Hamulus proximal to body different and located distinctly away from others (at least by a distance equal to its own length).
   2. Three hamuli morphologically similar and located equidistant from each other.
53. Front ventral margin of the forewing (1/29, 2/29).
   0. Without distinct tuft of spines.
   1. With posteriorly directed tuft of spines near distal end of the coastal cell.
54. Length of postmarginal vein (2/31).
   0. Distinctly shorter than marginal vein.
   1. Longer than marginal vein.
55. Length of marginal vein (2/32).
   0. Longer: more than 4× the length of stigmal vein.
   1. Shorter: less than 4× the length of stigmal vein.

Characteristics of the metasoma:

56. Petiole structure (1/33).
   0. Anterior articulation distinct, petiole ventrally membranous.
   1. Both sternum and tergum sclerotized transversely or slightly elongated anterior ventral margin extended into the propodeum; anterior articulation not separated from the body.
   2. Anterior articulation separate from the body of the petiole ventrally; anterior ventral margin of the body expanded outside the propodeum.
   3. Anterior articulation distinctly separated from the body by a lamella, body variously elongated.
   4. Anterior articulation united with the extended anterior ventral surface of the petiole body; lamella absent.
   5. Anterior articulation separated from body which is distinct dorsally and ventrally and posterior ventral margin not distinctly separated from sternum of gaster.
   6. Anterior articulation distinctly separated from the body only dorsally.
57. Syntergum (1/34)
   0. Convex, seventh and eighth tergites completely fused.
   1. Roof-like, posterior dorsal edge of seventh tergite not fused to eighth tergite.
58. Petiole length (2/33).
   0. Distinctly longer than wide.
   1. Transverse, not visible from dorsal side.
   2. As long as wide; visible from dorsal side.
59. Lateral sulcus of first abdominal tergite (2/34).
   0. Absent.
   1. Present.
60. First and second abdominal tergites of females (2/35).
   0. Independent.
   1. United but line of fusion is distinct.
   2. United with no trace of the line of fusion.
61. Fifth metasomal tergite of the female (2/36).
   0. As long as the first tergites.
   1. Distinctly shorter than the first tergite.
62. Seventh metasomal tergite (2/37).
   0. Short and completely cover the ovipositor sheath.
   1. Elongated and completely cover elongated ovipositor sheaths.
   2. Short and do not cover elongated ovipositor sheaths.
   3. Slightly elongated and cover the ovipositor sheaths.
63. Surface of seventh tergite (2/38).
   0. Differently sculptured beyond cerci.
   1. uniformly sculptured.
64. Tufts of silvery hairs on abdominal tergites (2/39).
   0. Absent.
   1. Two lateral tufts on tergite five.
   2. Four lateral tufts on tergite five and six.
   3. Single continuous tuft on tergite five.
   4. Silvery hairs evenly distributed on tergites.
65. Posterior end of ovipositor sheath (2/40).
   0. Not curved downwards.
   1. Distinctly curved downwards.